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Freshwater and coastal migration patterns in the silver stage eel *Anguilla anguilla*

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ABSTRACT

The unimpeded downstream movement patterns and migration success of small female and male *Anguilla anguilla* through a catchment in North West Europe was studied using an acoustic hydrophone array along the River Finn and into the Foyle estuary in Ireland. Twenty silver stage *A. anguilla* (L_t range: 332-520 mm) were trapped 152 km upstream from a coastal marine sea lough outlet and internally tagged with acoustic transmitters of which 19 initiated downstream migration. Migration speed was highly influenced by river flow within the freshwater compartment. *Anguilla anguilla* activity patterns were correlated with environmental influences; light, tidal direction and lunar phase all influenced initiation of migration of tagged individuals. Migration speed varied significantly between upstream and lower river compartments. Individuals migrated at a slower speed in transitional water and sea lough compartments compared with the freshwater compartment. While 88.5% survival was recorded during migration through the upper 121 km of the river and estuary, only 26% of *A. anguilla* which initiated downstream migration were detected at the outermost end of the acoustic array. Telemetry equipment functioned efficiently, including in the sea loch, so this suggests high levels of mortality during sea lough migration, or less likely, long-term sea lough residence by silver *A. anguilla* emigrants. This has important implications for Eel Management Plans (EMP's).

Key words: Anguillidae, migration triggers, survival, sea lough, telemetry.

INTRODUCTION

In the last 30 years the panmictic European eel *Anguilla anguilla* (L. 1758) population (Als *et al.*, 2011) has experienced declines across its range (ICES, 2013), the causes of which are not fully understood (Kettle *et al.*, 2011). An important precursor to any effective management of the existing population is to identify bottlenecks to critical life history stages. As a result of this decline, the European Union enacted legislation (EC Reg 1100/2007) to ensure increased *A. anguilla* escapement of the freshwater feeding lifecycle stage, the aim being to raise the biomass of potential semelparous spawners leaving continental waters for the spawning migration; the presence of newly hatched larvae in the south west Sargasso Sea in the western Atlantic reveals that to be the spawning area of the species (Schmidt, 1923; Kleckner & McCleave, 1988). The growth phase for *A. anguilla* in continental waters ends with a transition called the silvering process (Tesch, 2003; Durif *et al.*, 2005), following which *A. anguilla* residing in freshwater begin migrating towards marine waters. The downstream migration patterns in *A. anguilla* are thought to vary across localities (Vøllestad *et al.*, 1994; Breukelaar *et al.*, 2009). The majority of the information on silver stage *A. anguilla* migration comes from commercial fishing data (Durif & Eile, 2008) and consequently details of silver stage *A. anguilla* behaviour as they transit from freshwater to saltwater are poorly understood.

Tracking technologies allow detailed studies of individual migration behaviour in freshwater and inshore marine environments (Aarestrup *et al.*, 2010; Davidsen *et al.*, 2011; Verbiest *et al.*, 2012). Several studies have revealed impacts of hydropower impoundment and fisheries on riverine survival of migrating silver stage *A. anguilla* (Winter *et al.*, 2006; Travade *et al.*, 2010). The freshwater -marine transition represents an important life history stage for diadromous fishes. During the transition they experience fundamental physiological challenges at the freshwater - saltwater interface and there is evidence of increased mortality

risk from predators as migratory fishes enter sea water (Aarestrup *et al.*, 2010; Davidsen *et al.*, 2011; Aarestrup *et al.*, 2014). In common with other diadromous fishes, migrating silver stage *A. anguilla* pass through productive estuarine habitats which often have large numbers of avian, mammalian and fish predators. Predation pressures in such habitats may be high on migratory fishes, for example Keller (1995) reports that cormorants (*Phalacrocorax* sp.) a common species in estuarine habitats, feed heavily on smaller *A. anguilla*. Knowledge of escapement success during the freshwater saltwater transition is crucial to understanding of the natural dynamics of *A. anguilla* populations. Specifically, understanding migration behaviour, life stage specific mortality and ultimately migration success at this important life stage, is critical to effective conservation management. Recent work on downstream migration patterns has indicated low survival rates during migration to the open ocean (Verbiest *et al.*, 2012; Aarestrup *et al.*, 2010). However these studies were conducted in catchments impacted by hydropower and fisheries thus it is difficult to disentangle natural mortality from anthropogenic mortality resulting from hydroelectric power generation or fishery pressure. Furthermore the migration of male *A.anguilla*, which migrate at a smaller size than female *A. anguilla* (Poole *et al.*, 1990), is particularly poorly understood. Previous studies have focused solely on the behaviour of females (which are preferred for tagging as a result of being large relative to tag size) and as a result, field data on the downstream migration of smaller sized female and male *A. anguilla* is lacking. The aims of this study were to (i) determine the progression rates and migration behaviour of small silver stage *A. anguilla* through sequential catchment compartments; (ii) elucidate migration influences and how they may differ between catchment compartments; (iii) quantify escapement success of tagged individuals through freshwater and coastal sea lough habitats.

MATERIALS AND METHODS

STUDY AREA

The study was conducted in the Foyle catchment, Northern Ireland in 2013. The Foyle Catchment has an area of 4450 km² and drains into the Atlantic Ocean on the North coast of Ireland (55.01°N , 7.08°W). The River Finn has no man-made barriers to migration and the hydrology retains high natural variability. The sea lough (Lough Foyle) located at the mouth of the River Foyle is typical of an enclosed broad, but shallow, productive estuary and the exit point to the open ocean at Magilligan Point is narrow (0.98 km) (Fig.1). The upper limit of tidal influence is located 60 km from Magilligan Point and the salt wedge occurs approximately 40 km upstream of Magilligan Point depending on the tide and river flow conditions. In this study, the catchment compartments were designated as follows: freshwater (95 km long), transitional (26.8 km long) and sea lough (30.2 km long). Catchment characteristics are presented in Table I.

FISH CAPTURE AND TAGGING

Migrating silver stage *A. anguilla* were captured using a fixed fyke net (leader length=8.5 m, depth=55 cm , mesh=10 mm) in the outflow stream from Lough Finn at the source of the River Finn (54.50°N 8.05°W) between 29 September and 28 October 2013. Prior to measuring and tagging, *A. anguilla* were placed in a tank and anaesthetised with clove oil (0.5 mg⁻¹ of freshwater). After anaesthetisation, the total body length (L_T mm), mass (g), eye diameter (mm) and length of the pectoral fin (mm) were recorded to determine their maturation stage and sex according to Durif *et al.* (2005) (Table II). According to this classification, 17 *A. anguilla* were deemed mature males and three mature females (Table II). Fat content was measured on live individuals using a Distell FM 692 fat meter (Distell Meters, Scotland UK; www.distell.com). This meter has a micro strip sensor which measures the water content of a sample. The fat content of the fish is correlated with the water content and thus the measurement of one can determine the other if the relationship between the two is known. The fat meter was calibrated (company calibration) to the fat /water relationship

specific to *A. anguilla* prior to taking measurements. Three measurements were taken along the body on both sides of the *A. anguilla*. The fat meter was then used to calculate the average percent body fat for the individual based on the six readings.

A total of 20 silver stage *A. anguilla*, 17 males and 3 females (L_T range: 332-520 mm, mass range: 83-384 g) were tagged with individually coded acoustic transmitters (Model LP-7.3, 7.3 mm diameter, 18 mm length, 1.9 g mass in air, 139 dB re 1 μ Pa power, Thelma Biotel AS, Trondheim, Norway 2013; www.thelmabiotel.com) (Table II). For each *A. anguilla* an acoustic transmitter was surgically implanted through a 15 mm incision into the peritoneal cavity, and the incision closed with independent sterile sutures (6-0 ETHILON, Ethicon Ltd, Livingston, UK; www.ethiconproducts.co.uk). The mean tag to body mass ratio was $1.53 \pm 0.5\%$ (<2% recommended, *sensu* Lucas & Baras, 2000). *Anguilla anguilla* were aspirated with 100% river water throughout the procedure. Tags were programmed to have an acoustic transmission repeat cycle of $30 \text{ s} \pm 50\%$, giving a tag life span in excess of 110 days. This surgical procedure does not adversely affect behaviour of tagged *A. anguilla* (Thorstad *et al.*, 2013). Once the tagging procedure was complete, *A. anguilla* were returned to a recovery tank filled with highly aerated water. The entire surgical process took less than 4 minutes. After complete recovery (10-15 min), defined as orientation regained and response to stimuli, *A. anguilla* were released.

ACOUSTIC TRACKING

The passage of tagged *A. anguilla* was recorded using seven automatic listening stations (ALS: VEMCO VR2 W (vemco.com); Fig. 1.) deployed prior to tagging (August 2013) and recovered in February 2014. Detection ranges were tested for all ALSs to ensure all tagged *A. anguilla* passing ALS sites would be recorded. Range testing was conducted in freshwater and transitional compartments with varying hydromorphological conditions. No *A. anguilla*

were recorded on a downstream ALS which had not been previously recorded at inward ALSs higher in the catchment. Extensive range tests were undertaken for ALS at Magilligan Point (the sea lough sites; Fig.1.) to ensure coverage at these points was adequate to determine escapement success. To test for acoustic breaches at the final ALS an acoustic transmitter (Model LP-7.3, 7.3mm diameter, 18 mm length, 1.9 g mass in air, 139dB re 1 μ Pa power, Thelma Biotel AS, Trondheim, Norway 2013) was immersed at 3 m depth and trolled (~1500 m x 4; ebbing and flooding tide) by a drifting boat (engine off). Range tests revealed an acoustic range of 450 m ensuring overlap between the two final ALS (6&7), no acoustic breaches were recorded during range tests.

MIGRATION DESCRIPTORS

The ALS array was used to examine behavioural differences in migration patterns of *A. anguilla* during their downstream migration. Nineteen out of the 20 *A. anguilla* transmitters were detected at ALS1 (0.5km from release), it is assumed that these *A. anguilla* had initiated downstream migration. Freshwater compartment (FW) migration is defined as movement of tagged fish from the most upstream receiver ALS 1 downstream to ALS 2 at the point of tidal interface. It was assumed that *A. anguilla* which were detected at the first upstream receiver (ALS 1) but not detected entering the estuary (ALS 2) either terminated their migration or suffered mortality or tag failure in the freshwater compartment. Transitional water compartment migration was defined as the movement of *A. anguilla* between ALS 2 and ALS 4&5. Similarly *A. anguilla* which were detected at ALS 2 but not at ALS 4 and 5 were assumed to have terminated their migration, suffered mortality or tag failure in the transitional compartment. Sea lough compartment migration was defined as movement between ALS 4 and 5 and the lough exit at ALS 6 and 7. Tagged individuals were deemed successful migrants (*i.e* successful transit between the freshwater, transitional and sea lough compartments) if they were detected passing ALS 6 or 7 and thus entering the open ocean.

For migrating *A. anguilla*, transit time and travel speed between ALSs were calculated. The transit time corresponds to the time elapsed between the departure from an ALS, i.e, the last detection at that ALS, and arrival at the next, i.e, the first detection at the successive downstream ALS. Distance travelled between detection sites was calculated using the centre line of the river using ARC GIS software and was expressed in km day⁻¹.

ENVIRONMENTAL DATA

River discharge data were provided by the Office of Public Works, Ireland. Mean daily discharge from the River Finn was used to assess flow conditions for the study period in 2013. Tidal range data were obtained from published data (www.tidetimes.org.uk). Light level was defined as day or night, based on the times of sunrise and sunset, these were calculated using the NOAA sunrise/sunset calculator (NOAA, 2014). The lunar cycle was categorised into eight phases: new moon, waxing crescent, 1st quarter, waxing gibbous, full, waning gibbous, 3rd quarter, waning crescent based on the percentage of the moon illuminated using the R package lunar (Lazaridis, 2015).

DATA ANALYSIS

Differences in the number of successful migrants moving through successive compartments were tested using a Pearson chi-square test. Migration speed was log₁₀ transformed to reduce heterogeneity of variances. Differences in migration speed through compartments were tested by ANOVA. To investigate the potential factors influencing migration speed of individuals through the catchment a general linear model approach was taken. Migration speed (log₁₀ km d⁻¹) in freshwater, transitional water and sea lough compartments was modelled using *A. anguilla* *L_T*, body fat and water discharge as predictor variables. Final models were generated with non-significant variables being dropped. Model diagnostics were assessed graphically by examining the residuals for heterogeneity. A *t*-test was used to test for significant

differences between migration speeds of successful and unsuccessful migrants. Pearson chi square tests were used to test for differences in diurnal, lunar phases and tidal cycle (ebb or flood) effects on movement activity. Movement activity times were defined as the difference between detection time when entering receiver range and the time of the last detection before leaving receiver range. All analyses were performed using R statistical software 3.1 (R Core Team 2014).

RESULTS

MIGRATION SUCCESS

The 19 tagged *A. anguilla* which initiated downstream migration (detection at ALS 1) were all detected at the lower end of the freshwater compartment (ALS 2), thus 100% of migrants made successful passage through the freshwater compartment (Fig. 2, and 3). Seventeen *A. anguilla* (89%) were detected at the lower end of the transitional water compartment (ALS4-5). Of the 17 *A. anguilla* that entered the sea lough compartment, five *A. anguilla* (29%) were detected at ALS6-7 indicating successful passage through this zone (Fig. 2). Thus, overall there was 26% escapement of tagged *A. anguilla* to the open sea. There was a non-significant difference in migration success (assuming that non-detected tags at downstream loggers represent successful passage of tagged *A. anguilla*) between freshwater and transitional water compartments ($\chi^2 = 0.054$, $df=1$, $P > 0.05$). Estimated survival rates of tagged individuals were significantly lower in the sea lough compartment compared to the transitional compartment ($\chi^2 = 10.31$, $df=1$, $P < 0.001$) (Fig. 2).

MIGRATION INFLUENCES

Migration patterns of individuals were significantly related to environmental factors in some compartments. A general linear model revealed a significant relationship between discharge and migration speed in the freshwater compartment ($F_{1,17}=8.761$, $r^2=0.35$, $P < 0.05$) and

transitional water compartment ($F_{1,15}=5.058$, $r^2=0.26$, $P<0.05$) but not through the sea lough compartment ($F_{1,4}=8.761$, $r^2=0.02$, $P>0.05$). The number of downstream movements was also significantly higher at night than during the day through all three compartments; freshwater compartment ($\chi^2=35.103$, $df=1$, $P<0.001$), transitional compartment ($\chi^2=36.250$, $df=1$, $P<0.0001$) and sea lough compartment ($\chi^2=5$, $df=1$, $P<0.05$). The number of downstream movements was significantly different between tidal phases; a higher proportion of movements occurred during ebb tides (92.3%) in comparison to flood tide (7.6%) ($\chi^2=32.362$, $df=1$, $P<0.001$). A significantly higher number of *A. anguilla* movements (77.7%) were observed in the three moon phases which represent the least illumination during the lunar phase, waning crescent, new moon and waxing crescent compared with higher illuminated phases ($\chi^2=135.067$, $df=7$, $P<0.001$).

MIGRATION SPEEDS

Of the 19 tagged *A. anguilla* for which directional migration was recorded, all progressed downstream, no individuals detected at ALS 1 were recorded moving back upstream. Time spent from release to last detection on the outermost receivers ranged from 11 to 80 days for migrants. Overall the mean migration speed (km d^{-1}) of individuals was not found to be significantly influenced by *A. anguilla* L_T ($F_{3,37}=1.905$, $P>0.05$). Mean migration speeds were significantly different between compartments (ANOVA; $F_{2,38}=13.77$, $P<0.001$, Table III), specifically, slower migration speeds were observed in the transitional compartment compared with the freshwater compartment (Tukey HSD $P<0.001$) and between the sea lough compartment and the freshwater compartment (Tukey HSD $P<0.001$). However there was no difference in migration speeds between transitional and sea lough compartments (Tukey HSD $P>0.05$) (Fig. 3). Mean migration speed of migrants successfully reaching the open sea was not significantly different from unsuccessful migrants in the transitional compartment, freshwater compartments or sea lough ($P>0.05$ in all cases). Overall the level

of fat deposition did not significantly influence migration speed through freshwater and transitional compartments ($P>0.05$). The level of fat deposition was found to have a significant positive effect on migration speed of migrants through the sea lough ($t=5.204$, $_{1,3}$, $P<0.001$).

DISCUSSION

This study details differences in migration success and behaviour of small silver stage *A. anguilla* as they migrate down a freshwater river reach, through a transitional zone and into a coastal marine sea lough. The *A. anguilla* in this study (L_T range: 332-520 mm) exhibited a marked decline in migratory speed in the lower reaches of the catchment. Also shown are substantially higher losses of migrating *A. anguilla* in the sea lough compartment compared with freshwater and transitional water zones. While high mortality has been reported for downstream migrating larger female silver stage *A. anguilla* (Aarestrup *et al.*, 2010; Davidsen *et al.*, 2011), it has not been recorded for male and smaller female *A. anguilla*, nor in a catchment exhibiting a natural hydrology and free of anthropogenic influences (hydropower facilities and fisheries). These results strongly suggest that passage through a coastal marine sea lough imposes a high mortality rate on the seaward escapement of smaller *A. anguilla*.

MIGRATION SUCCESS

The detection of 26% of the tagged individuals which initiated downstream migration at the final array is a minimum estimate of successful escapement of tagged individuals. There are three possible explanations for the very low rate of detection of tagged *A. anguilla*.

Acoustic equipment failure or tag loss by A. anguilla; It is plausible that low detection efficiency resulting from poor receiver performance and or tag failure / performance may have resulted in low detection of tagged *A. anguilla* that reached ALS 6 or 7. The former is

highly unlikely as no acoustic breaches were recorded during range tests at the outer ALS array, ruling out the likelihood of potential non detection at the final listening stations. Additionally all receiver detections of individual *A. anguilla* recorded more than one signal. All *A. anguilla* transmitters had an estimated battery end life in late February and given that *A. anguilla* are estimated to arrive at spawning grounds from March-June (Tesch, 2003; van Ginneken & Maes, 2005; Aaerstrup *et al.*, 2009) it was expected that tag life should have been long enough to allow tagged *A.anguilla* to have emigrated before battery failure. Manufactures reported tag failure rate in tests are <1% and studies using the same tags, over the same period, have reported control tag failure rates in field environments of 0% (Gauld *et al.*, 2013). There was no evidence of impaired migration related to tagging with ~90% of tagged *A. anguilla* successfully migrating through the freshwater compartment and transitional compartments. Silver stage *A. anguilla* have been successfully surgically tagged in numerous other studies (Aaerstrup *et al.*, 2008, 2010; Davidsen *et al.*, 2011; Verbiest *et al.*, 2012; Bultel *et al.*, 2014) and surgical tagging of *A. anguilla* in a similar manner to the present study was not deemed to significantly affect behaviour post tagging of *A.anguilla* (Thorstad *et al.*, 2013) although osmotic stress encountered by tagged *A. anguilla* when moving from fresh to salt water warrants further research.

Settlement; A possible interpretation of migration patterns shown here, which has been raised by other studies is that sea migration could be a two-step migration process (Durif *et al.*, 2005; Aaerstrup *et al.*, 2008; Béguer-Pon *et al.*, 2014; Stein *et al.*, 2015). It has been reported that *A. anguilla* maturation may be more flexible than originally thought (Svedäng & Wickström, 1997) and that individuals may have the ability to interrupt migration and begin feeding again. Crook *et al.* (2014) demonstrated extended estuarine residence time for *Anguilla australis*, highlighting the possibility of more complex migration behaviour instead of the rapid and direct seaward migration originally assumed. Stein *et al.* (2015) also

highlighted the possibility that *A.anguilla* may need more than one migratory season to reach the sea and may temporally revert to a non-migratory stage. Therefore, it is possible that a proportion of the tagged *A. anguilla* in this study ceased their migration in the lower Foyle and began feeding again to commence migration at a later date.

Mortality; The most probable explanation is that *A. anguilla* in this study experienced high mortality in the sea lough and the low escapement rate observed in this study represents true escapement of migrating *A. anguilla* (or a combination of the above factors). Thus, the results from this study strongly suggest substantial mortality of silver stage *A. anguilla* during the period they are in coastal marine habitat, even in the absence of a fishery. These findings are similar to those of Aarestrup *et al.* (2010) who also reported significant losses of tagged female *A. anguilla*, interpreted as mortality during the early marine phase. Due to the high fat content (van Ginneken *et al.*, 2000) and their relative abundance, *A. anguilla* are a very profitable prey source for avian, fish and mammalian predators (Keller, 1995; Knöesche, 2003; Britton *et al.*, 2006; Lundström *et al.*, 2010; Béguer-Pon *et al.*, 2012). Productive estuarine habitats are home to numerous potential fish predators, and such predators could represent an important and unappreciated source of *A. anguilla* mortality which has important management implications.

MIGRATION INFLUENCES

An important environmental influence initiating migration in both freshwater and transitional compartments was increased water discharge. Increased discharge has been identified as initiating downstream movement in *A. anguilla* (Vøllestad *et al.*, 1986; Feunteun *et al.*, 2000). In the study presented here, this effect was clearer for *A. anguilla* migrating through the freshwater reaches and although evident also in the estuary (transitional compartment) the effect was considerably less pronounced. In the sea lough, the effect of water discharge on

movement disappeared. Aarestrup *et al.* (2010) noted a similar effect of declining migration responses to river discharges with passage downstream of the silver stage *A. anguilla* suggesting that tidal currents may possibly buffer the effect and this is consistent with the pattern in the current study. Selective tidal stream transport (STST) has been proposed as a mechanism influencing *A. anguilla* migration (McCleave & Arnold, 1999) which allows *A. anguilla* to quickly move through areas utilising tidal currents. The study presented here indicates that *A. anguilla* may exploit outgoing tidal currents while migrating in the transitional and sea lough compartments with 92% of migration initiations occurring at these times. This concurs with findings by Béguyer-Pon *et al.* (2014) who reported that American silver eels (*Anguilla rostrata* L.) use nocturnal ebb tide transport to migrate out of the St. Lawrence estuary. The *A. anguilla* in the present study also exhibited increased movement activity on phases around a new moon, with the majority of movements occurring in the lead up to a new moon, suggesting that migration is preferred on nights of the lowest lunar illumination.

In this study, most (94%) migratory movements of tagged *A. anguilla* occurred during the night, even when moving through the relatively turbid lower reaches of the river and estuary. Resident *A. anguilla* tracking studies have also shown activity peaks at night (Hedger *et al.*, 2010, Walker *et al.*, 2014). This pattern for smaller females and male *A. anguilla* has been found in other studies in freshwater (Vøllestad *et al.*, 1986; Tesch, 2003) and for coastal marine habitats in large female *A. anguilla* (Davidsen *et al.*, 2011; Aarestrup *et al.*, 2008, 2010). Predation has long been implicated as a major selective force in the evolution of several behavioural characteristics of animals (Lima & Dill, 1990). The migration influences noted in this study are probably an evolutionary response to predation pressures. *Anguilla anguilla* are an important food source for predators (Keller, 1995; Knöesche 2003; Britton *et*

al., 2006; Lundström *et al.*, 2010; Béguer-Pon *et al.*, 2012). One such predator, cormorants (*Phalacrocrax* sp.) are visual foragers, feeding during daylight and twilight hours (Siegfried *et al.*, 1975) and higher *A. anguilla* movements on nights with reduced lunar illumination observed in this study are probably indicative of predator avoidance behaviour, which reduces the likelihood of encountering predators when undertaking their downstream migration (Fuiman & Magurran, 1994).

MIGRATION SPEED

The migration speed of individuals through the catchment was not influenced by L_T . This contrasts with findings by Verbiest *et al.* (2012) and Bultel *et al.* (2014) who reported faster migration progression of larger individuals. Inter- individual variability in migration speeds was apparent across compartment types, however ultimate migration success was not affected by individual migration speed through the catchment. Overall migration speed was found to be significantly higher in the upper reaches in comparison to the lower reaches of the study catchment. This contrasts with the findings of Aaerstrup *et al.* (2010) who found slower progression rates upstream in comparison to downstream reaches in large female *A. anguilla*. Given that tagged *A. anguilla* in this study ranged from 332-520 mm in comparison to Aaerstrup's study (560-840 mm), the contrasting results may be due to size or sex differences of tagged *A. anguilla*. Thus, the fresh-saltwater transition may possibly take longer for smaller sized *A. anguilla*. Bultel *et al.* (2014) also noted a slower migration speed in the downstream catchment compartments and suggested reduced progression may be a result of very strong salinity gradients. Such gradient transfers can be found in large estuaries similar to that in this study. The salinity gradient changes quickly in the lower Foyle ranging from 0.14- 25.50 over 20 km, which may explain the reduced migration speed. Thus one can postulate that reduced migration speed in lower compartments could be related to an

acclimatization process due to increased salinity levels, and potential physiological size related factors.

CONCLUSIONS

This study strongly suggests previously unreported poor survival through coastal marine habitat of small female and male silver stage *A. anguilla* (340-520 mm), though with the possibility that low recorded escapement could reflect long-term sea lough residency by a high proportion of small silver stage *A. anguilla* emigrants. More detailed research is needed to differentiate between these possibilities. If the low level of recorded escapement is due to mortality, coastal sea loughs may be a potential bottleneck to *A. anguilla* escapement and potential mortality through such zones should be considered in models estimating production from a system. Given the smaller size of tagged *A. anguilla* in this study, it is hypothesised that predation pressure may be high on this size component and thus significantly influence escapement success. Given the likely scale of the effects identified here, estuarine and coastal migration processes may be having very significant effects on the long term dynamics of *A. anguilla* populations if this pattern is replicated elsewhere. More information is urgently needed.

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542 FIGURE 1. Map of study site, compartment types marked with grey boundary line,
543 FW=freshwater, TW=transitional. ALS refers to Acoustic Listening Station outlined by solid
544 dots.

545 FIGURE 2. Proportion of tagged *A. anguilla* detected through catchment compartments
546 defined as freshwater (FW), transitional water (TW), and sea lough (SL). Distance 0 is the
547 release point.

548 FIGURE 3. Migration speed (km d^{-1}) through catchment compartments. FW= freshwater,
549 TW= Transitional compartment, SL=Sea lough.

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551 TABLE I. Environmental variables in compartments through catchments.

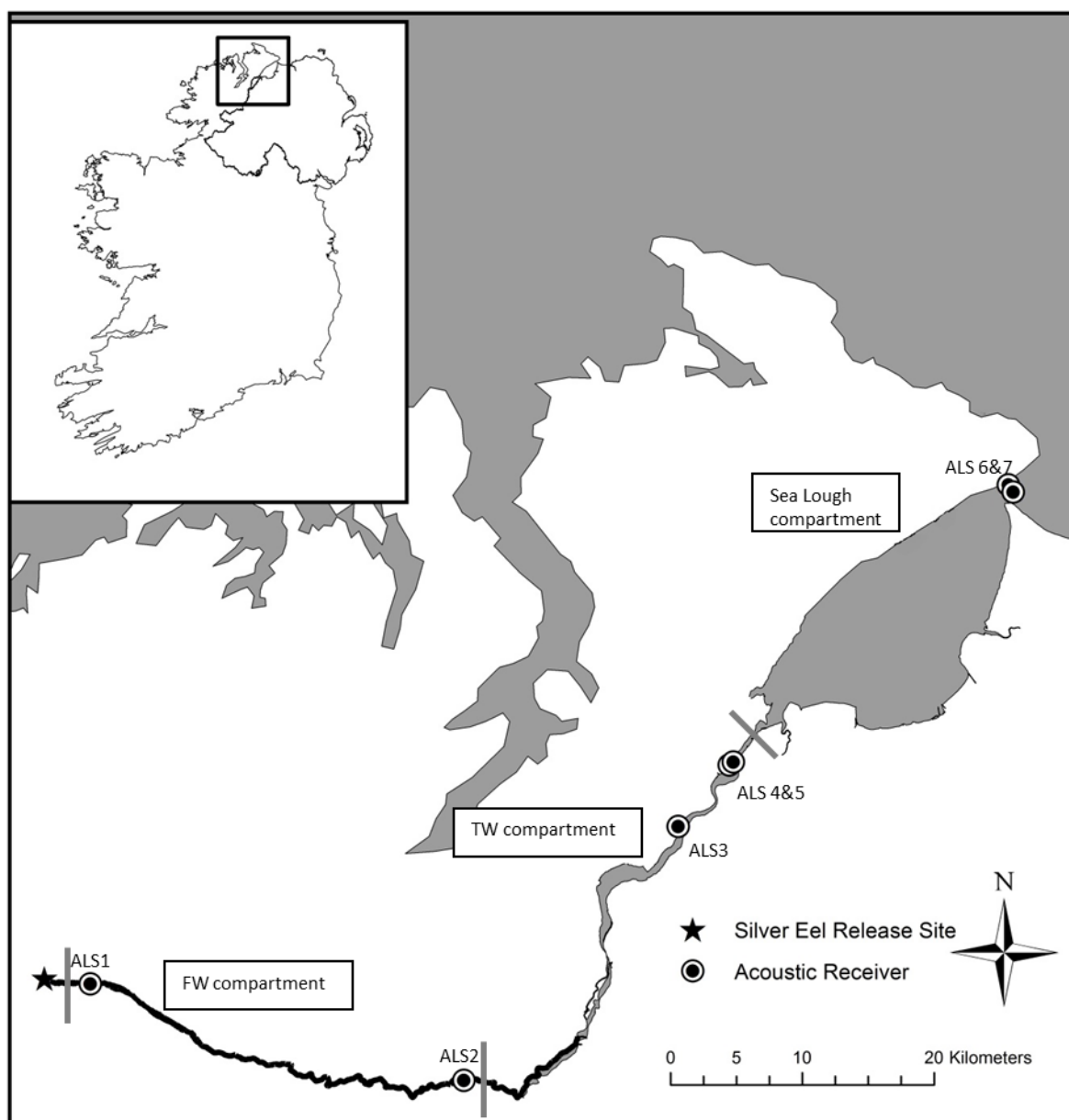
Variable	Freshwater	Transitional	Sea Lough
Salinity PSU (range)	-	0.14- 28.41	29.63- 32.20
Dissolved oxygen (mg l ⁻¹) ± S.D	-	8.10±0.65	8.04 ± 0.15
Mean Depth (m) ± S.D	-	2.58±0.86	3.12±1.49
Length (Km)	95	26.88	30.22

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554 TABLE II. Characteristics of tagged individuals. **Successful migrants detected passing final array.
555 Silver Index (*sensu* Durif *et al.*, 2005) MII = mature males, FV = mature female. ALS 1 refers to
556 Acoustic Listening Station 1.

I.D	L_T (mm)	Mass (g)	Fat (%)	Silver Index	Release date	Detection span from ALS 1 (days)
2585	354	72	29.8	MII	06/10/2013	5.14
2577	365	79	30	MII	05/10/2013	8.14
2575	354	82	22.9	MII	05/10/2013	80.14**
2592	332	83	28.4	MII	08/10/2013	5.15
2583	360	84	22.9	MII	06/10/2013	5.06
2581	360	86	30.6	MII	08/10/2013	5.97
2586	365	92	26.6	MII	28/10/2013	11.27**
2593	365	96	21.9	MII	04/10/2013	2.91
2576	350	97	26.3	MII	08/10/2013	43.15**
2578	384	99	23.6	MII	08/10/2013	62.87
2579	400	100	28.0	MII	28/10/2013	16.59
2588	394	105	26.0	MII	28/10/2013	3.01
2582	401	110	28.0	MII	29/09/2013	3.95
2587	395	115	30.0	MII	05/10/2013	19.69
2589	410	126	22.6	MII	08/10/2013	22.93**
2584	435	129	26.8	MII	05/10/2013	-
2580	442	249	29.6	MII	28/10/2013	10.17
2590	530	280	21.7	FV	29/09/2013	36.43
2591	520	320	22.0	FV	29/09/2013	2.99
2574	515	384	24.5	FV	02/10/2013	48.9**



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559 FIGURE 1

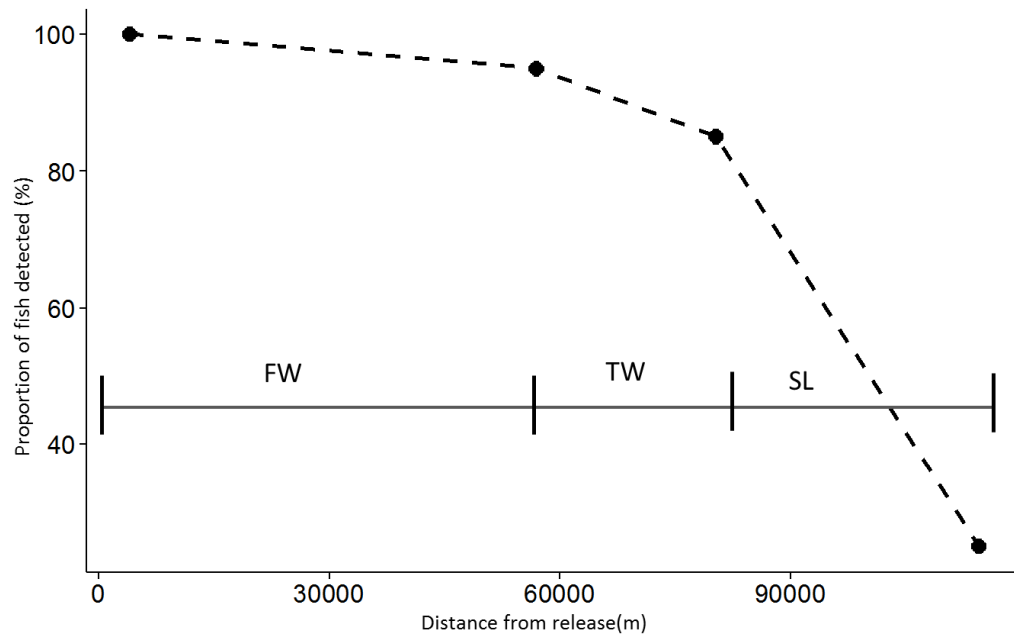


FIGURE 2.

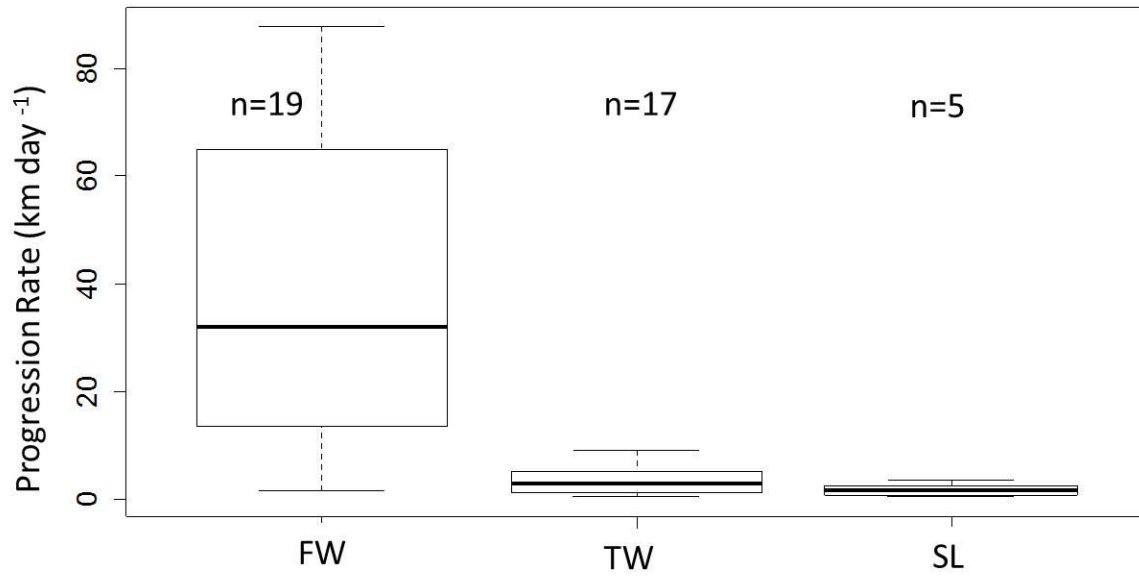


FIGURE 3.

TABLE III. Mean migration speed (mean \pm S.D; parentheses: range) in compartment types, n = number of *A. anguilla* monitored in a given compartment.

	<i>n</i>	Distance (km)	m/s ⁻¹	km/day ⁻¹
Freshwater	19	95	0.45 \pm 0.36 (0.01-1.01)	39.18 \pm 31.84 (1.58-87.7)
Transitional	17	26.88	0.04 \pm 0.03 (0.005-0.11)	3.42 \pm 2.68 (0.42-9.21)
Sea lough	5	30.22	0.019 \pm 0.015 (0.006-0.04)	1.64 \pm 1.34 (0.55-3.48)

Total	0.19 ± 0.27 (0.005-1.01)	16.68 ± 23.97 (0.42-87.74)
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